The Characteristics of Five Species of Hollow-Bearing Trees on the New South Wales Central Coast

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Todarello, P. and Chalmers, A. (2007). The characteristics of five species of hollow-bearing trees on the New South Wales central coast. *Proceedings of the Linnean Society of New South Wales* **128**, 1-14.

Five native eucalypt species were examined to investigate the abundance, entrance size diameter and type (e.g. trunk, branch) of hollows present. A total of 698 living trees were sampled within 22 one hectare plots. The trees were distributed across five open forest or woodland communities on the Central Coast of NSW; these communities were underlain by Narrabeen or Hawkesbury sandstone. The number of hollows per tree was positively correlated with the diameter of the tree and, with the exception of *Corymbia gummifera*, with the height of the tree. The smallest species examined, *Eucalyptus haemastoma*, contained a high proportion (60%) of small diameter (20-35 cm) hollow-bearing trees, confirming that hollow availability is more strongly related to species characteristics rather than to absolute diameter. *Eucalyptus haemastoma* had the highest proportion of hollow-bearing trees (78%) followed by *Angophora costata* (40%), *Eucalyptus punctata* (26%), *C. gummifera* (24%) and *Eucalyptus pilularis* (22%). The results obtained for *E. pilularis* may not be a true reflection of the propensity of this species to form hollows, as the sampled population may have been affected by timber removal. Most hollows had small (2-5 cm) diameter entrances (47%) and occurred in branches (84%) rather than in main stems (16%).

Manuscript received 1 June 2005, accepted for publication 18 May 2006.

KEYWORDS: *Angophora costata, Corymbia gummifera, Eucalyptus haemastoma, Eucalyptus pilularis, Eucalyptus punctata*, cavities, habitat trees, hollows

INTRODUCTION

Gibbons and Lindenmayer (2002) estimate that there are over 300 native vertebrate species that use tree hollows within Australia. On the Central Coast of NSW there are at least 54 fauna species that use tree hollows, 13 of which are listed as threatened under the *NSW Threatened Species Conservation Act* 1995. For example, Smith and Murray (2003) found that the abundance of all possums and gliders in the Wyong region of the NSW Central Coast increased with the number of hollow-bearing trees, particularly in areas where the average diameter at breast height was greater than 80 cm. They also found that the highest estimated density of squirrel gliders (*Petaurus norfolcensis*) occurred in associations of Scribbly Gum (*Eucalyptus haemastoma*), Smooth-barked Apple (*Angophora costata*) and Red Bloodwood (*Corymbia gummifera*).

Many authors (Lindenmayer et al. 1991, 1993b, 1994; Cockburn and Lazenby-Cohen 1992; Eyre and Smith 1997; Lindenmayer 1997; Wormington et al. 2003) have shown that different species of arboreal marsupials exhibit preferences for hollow-bearing trees with different characteristics. Occupation of hollows by fauna is associated with hollow entrance diameter and hollow depth as these characteristics influence the degree of protection from predators, the micro-climate and the provision of sufficient space for sleeping and nesting (Gibbons et al. 2002; Gibbons and Lindenmayer 2002). While small animals generally prefer hollows with small entrances, they may also use hollows with large entrances. For example, *Antechinus* spp., feathertail gliders (*Acrobates pygmaeus*) and sugar gliders (*Petaurus breviceps*) prefer hollows with entrance widths of 2-5 cm, but will use hollows with entrance widths > 5 cm (Gibbons et al. 2002). Larger species such as the common ringtail possum (*Pseudocheirus peregrinus*), greater glider (*Petauroides volans*), yellow-bellied glider (*Petaurus australis*) and common brushtail possum (*Trichosurus vulpecula*) are restricted to hollows with a minimum entrance width of > 5 cm (Gibbons et al. 2002). Large forest owls and cockatoos require large hollows for breeding, which tend to only occur in large diameter trees (Gibbons and Lindenmayer 2002). For example, Gibbons et al. (2002) only recorded the Powerful Owl (*Ninox strenua*) in hollows with a minimum entrance diameter of > 10 cm. Fauna are more likely to occupy trees with many hollows because it is more likely that these trees will have a least one suitable hollow (Gibbons et al. 2002).

The combined factors of clearing for agriculture, forestry and urbanisation have all contributed significantly to the reduction of the forest estate (Lindenmayer et al. 1993a; Cork and Catling 1996). Unfortunately many of these cleared forests supported optimal habitat for hollow-dependent fauna (Norton 1987; Bennett et al. 1994). Further, of those species that inhabit wood production forests, arboreal fauna are considered the most vulnerable to the impacts of timber harvesting (Ball et al. 1999). Bennett et al. (1994) argue there is growing evidence that the availability of suitable hollows is a limiting factor for most hollow-dependent fauna. Hollow-bearing trees in managed stands may be reduced by about 50 – 90% of that found in 'natural' stands, a reduction predicted to reduce populations of hollow-using fauna as well as faunal diversity (Gibbons and Lindenmayer 2002).

Hollow formation in eucalypts results from a series of abiotic and biotic events following the wounding of living stem tissue (Wilkes 1982). Wounding can occur in a number of ways including branch breakage due to high winds and exposure to high temperatures during fire (Gibbons and Lindenmayer 2002). After wounding, the process of wood decay follows a complex succession of micro-organisms including bacteria, fungi and insects such as termites (Wormington et al. 2003; Wilkes 1982; Perry et al. 1985; Gibbons and Lindenmayer 2002). A hollow eventually forms when decay undermines the strength of a branch, or when a branch has broken off during strong winds and/or fire; and the hollow is subsequently excavated by fungi, termites and other invertebrates and animals (Gibbons and Lindenmayer 2002). Physiological stress and fire predispose trees to attack by fungi and termites, while fire is also directly involved in excavating hollows (Gibbons et al. 2002). It may take 120-220 years for hollows to form (Gibbons and Lindenmayer 2002).

The number of hollows in individual trees and the size of hollows generally increase as tree diameter increases (Bennett et al. 1994; Williams and Faunt 1997; Gibbons et al. 2000; Lindenmayer et al. 2000; Whitford 2002). Larger trees tend to have a greater number of hollows because trees become physiologically weaker and shed more branches as they age and are more likely to have been exposed to stochastic events (e.g. fire) that facilitate hollow formation (Gibbons et al. 2002; Gibbons and Lindenmayer 2002).

Despite the large number of fauna species that rely on tree hollows, there is a paucity of data on the distribution and abundance of hollows within Australia (Gibbons and Lindenmayer 2002). Little is known about the hollow characteristics of specific tree species occurring on the Central Coast of NSW. An understanding of the propensity of different tree species to form hollows in any given area or region is essential to manage and maintain the hollow tree resource for that area. Thus, the main aim of this study was to examine the number and type of hollows in five tree species (*Angophora costata* Britten, *Corymbia gummifera* (Gaertn.) K.D.Hill and L.A.S.Johnson, *Eucalyptus haemastoma* Sm., *Eucalyptus pilularis* Sm. and *Eucalyptus punctata* DC. subsp. *punctata*) common on the NSW Central Coast. With the exception of *E. pilularis*, no previously published information on hollows could be found for these species. More specifically, the study asked:

1. Does hollow abundance depend on tree size (diameter and height)?
2. Are there differences in the propensity of the species examined to form hollows?
3. Are there differences between the species in the location (main stem versus branch) and entrance size of hollows?

MATERIALS AND METHODS

Study area

The Central Coast region of NSW has a warm temperate climate and supports closed forests, tall open forests, open forests, woodlands and heath (Murphy 1993). Rainfall ranges from a high of 1310 mm along the coast at Gosford to a low of 740 mm at Bucketty in the northwest (Murphy 1993). In summer, the average monthly temperatures are highest (27.2°C) on the coast and lowest (15.2°C) on the plateau, while in winter, average temperatures are highest (19.7°C) on the coast and lowest (4.2°C) in the valleys (Murphy 1993).

The five vegetation communities sampled in this study were open forests or woodland found on infertile soils underlain by Narrabeen or Hawkesbury

Sandstone. They were: i) Coastal Foothills Spotted Gum- Ironbark Forest; ii) Dharug Roughbarked Apple Forest, which is found over a number of topographic positions on Narrabeen Sandstones and within the rain shadow of the Watagan Ranges; iii) Coastal Narrabeen Shrub Forest, which occurs on skeletal ridge-top soils often near or with outcroppings of Hawkesbury and Narrabeen Sandstone; iv) Exposed Hawkesbury Woodland, which generally occurs on crests, ridges and exposed slopes on sandy soils of the Hawkesbury Sandstone series; and v) Exposed Yellow Bloodwood Woodland, which is found on dry exposed, infertile ridges and slopes on Hawkesbury Sandstone (LHCCREMS 2000).

Site selection

Sites were selected based on the frequency of the target species within the 55 vegetation communities that occur within the Central Coast and Lower Hunter Region (LHCCREMS 1: 100 000 Vegetation Map Sheet 2003). To minimise sampling time and effort, preference was given to those vegetation communities that contained more than one of the target species at frequencies greater than 30% (Table 1). A total of five vegetation communities fulfilled this criterion. Sampling of the five target species was undertaken at 22 sites distributed within three National Parks and two State Forest reserves on the Central Coast (Fig. 1; Table 1). State Forest logging history records indicate that the four sites sampled in vegetation community 1 had been logged between 1966 and 1980-82. The two State Forest sites in vegetation community 3 had been logged between 1966 and 1999. For vegetation community 4, two of the State Forest sites had been logged between 1966 and 1984-85, whilst the other two sites were last logged in 1962 and 1965-66. Sites sampled at Bouddi National Park (vegetation community 3) may have been subject to timber removal by subsistence farmers prior to the land being added to the Park between 1938 and 1967 (Strom 1986).

The location of each site was randomly selected within each vegetation community using the following procedure. The distance of the main access

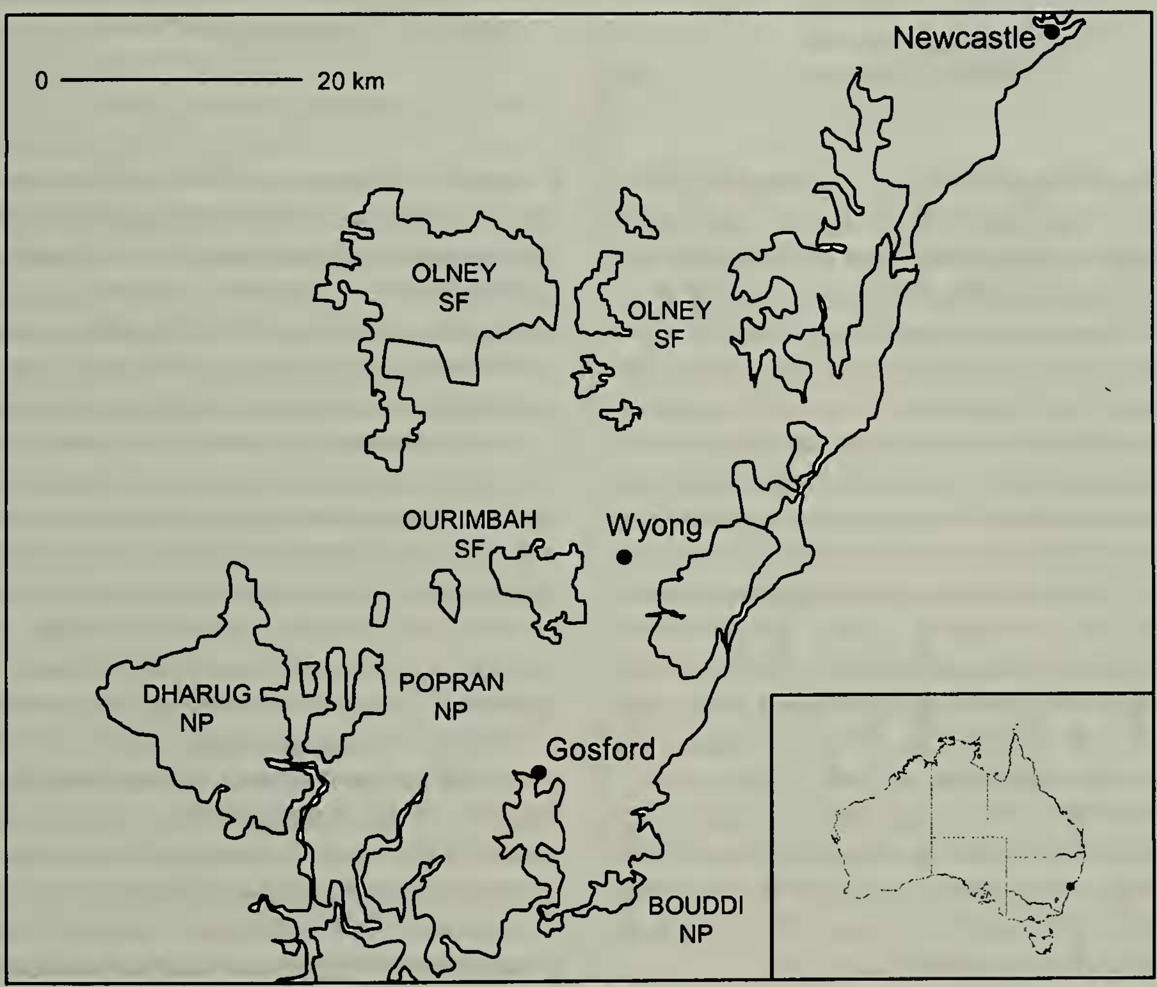

Figure 1. Location of the Central Coast of New South Wales (inset) and the three National Parks and two State Forests sampled in the current study.

Table 1. Vegetation communities sampled in the study, target species and their expected frequencies and number of sites by land tenure within each vegetation community. 1 – Coastal Foothills Spotted Gum-Ironbark Forest; 2 – Dharug Roughbarked Apple Forest; 3 – Coastal Narrabeen Shrub Forest; 4 – Exposed Hawkesbury Woodland: 5 – Exposed Yellow Bloodwood Woodland. * based on LHC-CREMS (2000)

Vegetation community*	Target species in each vegetation community	Frequency*	Land Tenure	No. of Sites
1	*Angophora costata*	36%	Ourimbah State Forest	2
	Eucalyptus punctata	31%	Olney State Forest	2
2	*Eucalyptus punctata*	68%	Dharug National Park	3
3	*Angophora costata*	74%	Ourimbah State Forest	2
	Eucalyptus pilularis	40%	Bouddi National Park	4
	Corymbia gummifera	48%		
4	*Angophora costata*	45%	Ourimbah State Forest	4
	Eucalyptus haemastoma	50%	Popran National Park	4
	Corymbia gummifera	75%		
5	*Eucalyptus punctata*	52%	Dharug National Park	1
	Corymbia gummifera	40%		

road running through the area to be sampled (portion of reserve containing one of the five vegetation communities) was measured from its entry to its exit point on a topographic map. Each 1 km section of the access road was allocated a number and numbers were randomly chosen to determine how many kilometres the site would be from the entry point of the reserve. A 100 m section of road was then randomly chosen from that 1 km section using the same procedure (with 100 m sample lengths). At each survey point a 1 ha (100 m x 100 m) quadrat was established 50 m off the access road. The side of the access road to be sampled was determined by flipping a coin. Quadrats were placed 50 m away from any existing road or track to minimise the influence of edge effects and disturbance created by road construction and maintenance. All quadrats were established at least 1 km apart to ensure the samples were independent of each other and would be representative of any variation within the vegetation. The placement of quadrats 1 km apart and 50 m from the road is consistent with the methods used by Gibbons et al. (2000).

Data collection

All living trees of the target species with a diameter at breast height (dbh) > 20 cm were sampled in each 1 ha quadrat. The lower limit of 20 cm dbh was chosen because previous studies in other regions (Williams and Faunt 1997; Whitford 2003; Wormington et al. 2003) have shown that hollow-bearing trees of this size contain hollows that may be used by the smaller marsupials. The diameter of each tree was measured using a diameter tape at a height of 1.3 m over bark and allocated to one of the following diameter classes: 20-35, 36-51, 52-67, 68-83 or >84 cm. Tree height was determined using a clinometer and each tree sampled was allocated to one of the following height classes: 5-10, 11-16, 17-22, 23-28 or >29 m. The number of hollows in each tree was determined from the ground using 10 mm x 25 mm binoculars. A hollow was defined as any cavity with an entrance > 2 cm in diameter and occurring > 3m above the ground. Entrances that were obviously 'blind' were not counted. 'Blind' was defined as "a branch stub or area of damage that does not lead to a cavity" (Gibbons and Lindenmayer 2002). Hollows in stumps or large fire scars (fissures) were not included. Each hollow was assigned as either having a small (2-5 cm), medium (6-10 cm) or large (>10 cm) entrance based on a visual estimate from the ground. The location of each hollow was recorded as either occurring in a branch or main stem. The lower size limit for sampling and the diameter, height and hollow classes were consistent with previous studies by Gibbons and Lindenmayer (1997), Williams and Faunt (1997), Gibbons et al. (2002) and Wormington et al. (2003).

Statistical analyses

The data were not normally distributed and transformation did little to improve normality. Therefore the Kruskall-Wallis test was used to determine whether there were significant differences between species in the ranked averages of the number of hollows per tree, tree density and density of hollow-bearing trees. Spearman rank correlations were used to test for an association between number of hollows and diameter, as well as between hollow number and tree height. All statistical analyses were conducted with SPSS version 11.5.

RESULTS

A total of 698 living trees were sampled across the five species, with 254 of these trees (36%) being hollow-bearing and 781 hollows being observed. Tree density of those species examined (i.e. not total tree density of a site) ranged from 1 to 37 trees ha^{-1} (mean of 16.6 ha^{-1}) and the number of hollow-bearing trees ranged from 0 to 27 ha^{-1} (mean of 6.2 ha^{-1}). Due to the composition of the vegetation communities sampled, there were considerably fewer data collected for *Eucalyptus pilularis* than for the other species (Table 2). *Angophora costata* and *E. pilularis* showed a similar range of tree diameters, but the mean diameter of *E. pilularis* was considerably larger than that of *A. costata* (Table 2). *Eucalyptus haemastoma* was the shortest species investigated, whilst *Eucalyptus punctata* was the tallest (Table 2). Of those species examined, *Angophora costata* showed the greatest range in height (Table 2).

The mean number of hollows per tree differed significantly between the tree species (K = 107.5; 4 df; $p < 0.0001$). *Eucalyptus haemastoma* had the highest mean number of hollows per tree, followed by *A. costata* and *E. pilularis*, while *E. punctata* and *Corymbia gummifera* had the fewest number of hollows (Table 2). *Eucalyptus haemastoma* had the highest proportion of hollow-bearing trees (78 %) followed by *A. costata* (40 %) > *E. punctata* (26 %) > *C. gummifera* (24 %) > *E. pilularis* (22 %). At the stand level (i.e. per ha), tree density did not differ significantly between the species (K = 1.5; 4 df; p= 0.820), although the density of hollow-

Table 2. The range of values for various attributes of tree stems and hollows for each of the five species examined in the current study. SE = standard error of the mean.

Variable	*Angophora costata*	*Eucalyptus punctata*	*Eucalyptus pilularis*	*Eucalyptus haemastoma*	*Corymbia gummifera*
No. of 1 ha quadrats with target species	11	8	5	7	11
Total no. of trees sampled	175	157	82	103	181
Total no. of hollows observed	211	105	97	255	113
Mean (± SE) tree diameter (cm)	35.7 ± 1.28	38.4 ± 1.45	51.8 ± 3.61	39.8 ± 1.35	33.8 ± 1.14
Range of tree diameter (cm)	20 - 147	20 - 124	20 - 151	21 - 85	20 - 86
Mean (± SE) tree height (m)	23.3 ± 0.53	27.6 ± 0.43	21.7 ± 0.41	12.7 ± 0.27	18.1 ± 0.34
Range of tree height (m)	10 - 39	18 - 39	16 - 32	7 - 21	11 - 32
Mean (± SE) no. of hollows per tree	1.2 ± 0.15	0.7 ± 0.12	1.2 ± 0.30	2.5 ± 0.20	0.6 ± 0.10
Mean (± SE) no. of trees ha^{-1}	17.0 ± 3.40	18.1 ± 1.78	16.2 ± 3.89	14.7 ± 1.44	16.5 ± 1.77
Mean (± SE) no. of hollow-bearing trees ha^{-1}	6.5 ± 2.48	5.9 ± 1.16	3.8 ± 1.88	11.0 ± 1.20	4.1 ± 1.34

Table 3. Spearman rank correlations between hollow number and tree diameter and hollow number and tree height for each individual species. * p<0.05; ** p< 0.01; ns = not significant (p>0.05).

	n	Spearman's rho	
		Tree diameter	Tree height
Angophora costata	175	0.61**	0.31**
Eucalyptus punctata	157	0.44**	0.32**
Eucalyptus pilularis	82	0.67**	0.40**
Eucalyptus haemastoma	103	0.58**	0.23*
Corymbia gummifera	181	0.53**	0.06^{ns}

bearing trees did (K = 10.7; 4 df; p < 0.05). The mean density of hollow-bearing trees was highest for *E. haemastoma* followed by *A. costata, E. punctata, C. gummifera* and *E. pilularis* (Table 2).

Hollow number and tree size

There was a significant positive association between tree diameter and number of hollows per tree for each of the five species examined (Table 3; Fig. 2). *Eucalyptus pilularis* formed few hollows in trees < 80 cm dbh (Fig. 2c) but had the highest count of hollows occurring in any one tree. That tree contained 15 hollows and occurred in the > 84 cm diameter class (Fig. 2c). With the exception of *Corymbia gummifera*, there was a significant positive association between tree height and number of hollows per tree for each of the species (Table 3). However, the relatively low Spearman's rho values (Table 3) and the scatter plots (Fig. 3) illustrate that the relationship between tree height and number of hollows was weak.

The proportion of trees that were hollow-bearing (i.e. at least one hollow) increased with increasing trunk diameter, and at least 80% of trees with diameters ≥ 84 cm were hollow-bearing (Fig. 4). The proportion of *Eucalyptus haemastoma* trees that were hollow-bearing was always greater than 60%, irrespective of diameter size class (Fig. 4). For *A. costata* and *E. haemastoma* all trees ≥ 68 cm in diameter were hollow-bearing (Fig. 4). *Eucalyptus pilularis* was the only species examined that had no hollow-bearing trees in the smallest (20-35 cm) diameter class (Fig. 4). Only a small number of *E. pilularis* individuals were sampled in the 52-67 cm and the 68-83 cm diameter classes (Fig. 4), thus any inferences about the lack of hollow-bearing trees in these size classes are tentative.

The mean number of hollows per tree increased with increasing trunk diameter and all of the five species had, on average, five or more hollows per tree once their diameter was ≥ 84 cm (Fig. 5). With the exception of *E. haemastoma,* trees with diameters between 20 cm and 51 cm had, on average, fewer than two hollows per tree (Fig. 5). Compared to the other species examined, *E. haemastoma* had a relatively high mean number of hollows per tree in the three smallest diameter classes (Fig. 5). In contrast, *E. pilularis* had a relatively low mean number of hollows in all but the largest size class. For *Angophora costata, Eucalyptus punctata* and *Corymbia gummifera*, the greatest increase in the mean number of hollows (more than double) occurred between the 68-83 cm and the ≥ 84 cm diameter classes (Fig. 5). The number of hollows per tree increased with tree height for *A. costata, E. punctata* and *C. gummifera* (Fig. 6). All of the *Eucalyptus haemastoma* trees that reached > 16 m in height had an average of five hollows per tree (Fig. 6).

Entrance size and location of hollows

Overall (across all species) there was a much higher prevalence of hollows with small entrances (47%) compared to those with medium (26%) and large (26%) entrances. *Angophora costata* had the highest proportion of hollows with small entrances, but the lowest proportion of hollows with medium and large entrances (Fig. 7). *Eucalyptus pilularis* had the lowest proportion of hollows with small entrances, while it had the highest proportion of hollows with large entrances (Fig. 7). However, the number of hollow-bearing *E. pilularis* trees sampled was relatively small. The other three species had similar hollow entrance size distributions, except that *E. punctata* had a higher proportion of hollows with large entrances compared to that of *E. haemastoma* and *C. gummifera* (Fig. 7).

There was a much higher prevalence of hollows in branches (84%) than in main stems (16%). *Angophora costata* (26 %) and *E. punctata* (24 %) had the highest proportion of main stem hollows, followed by *C. gummifera* (19 %), *E. haemastoma* (10 %) and

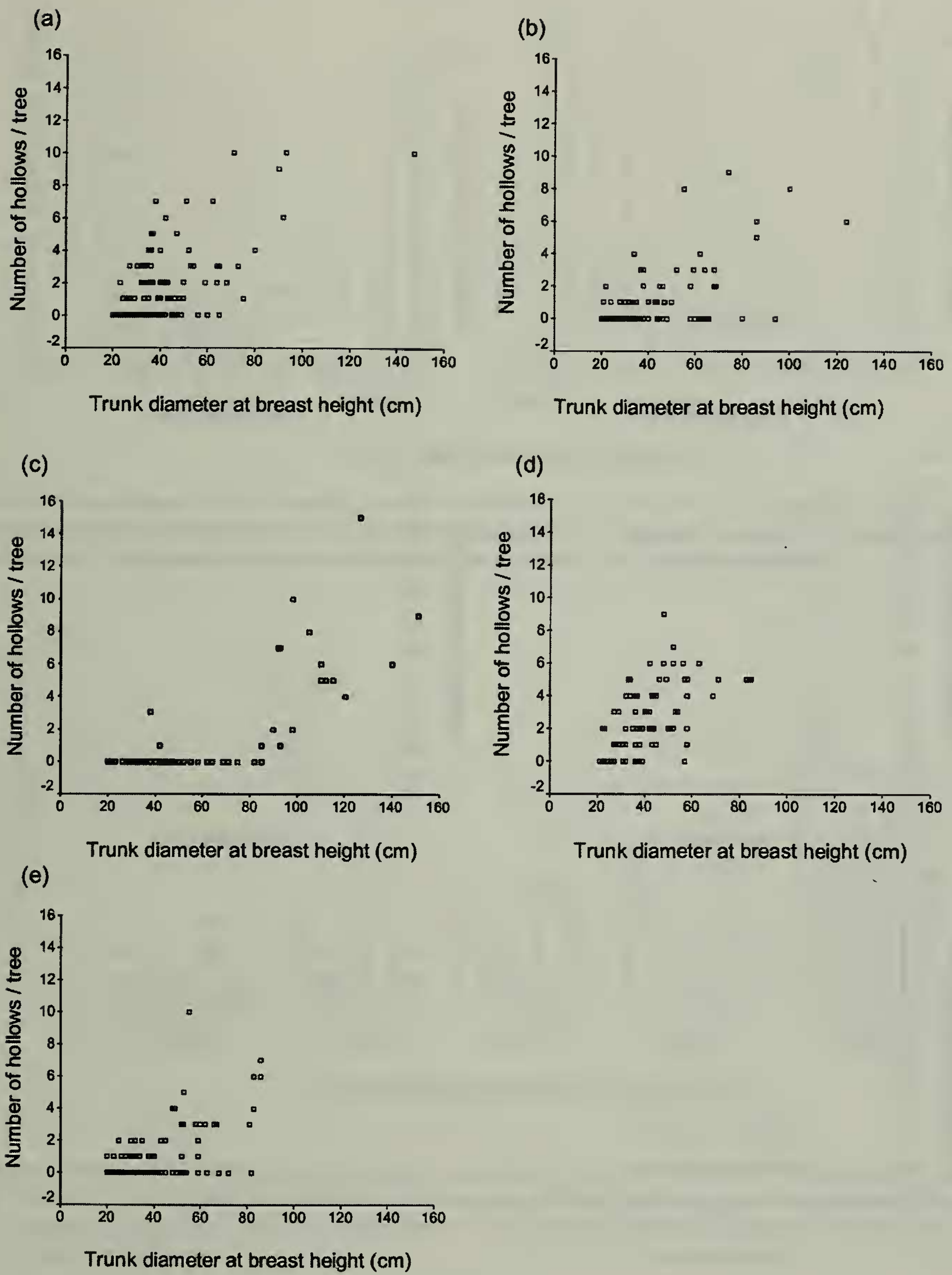

Figure 2. Scatterplots of number of hollows per tree against trunk diameter at breast height for (a) *Angophora costata*; (b) *Eucalyptus punctata*; (c) *Eucalyptus pilularis*; (d) *Eucalyptus haemastoma*; and (e) *Corymbia gummifera*.

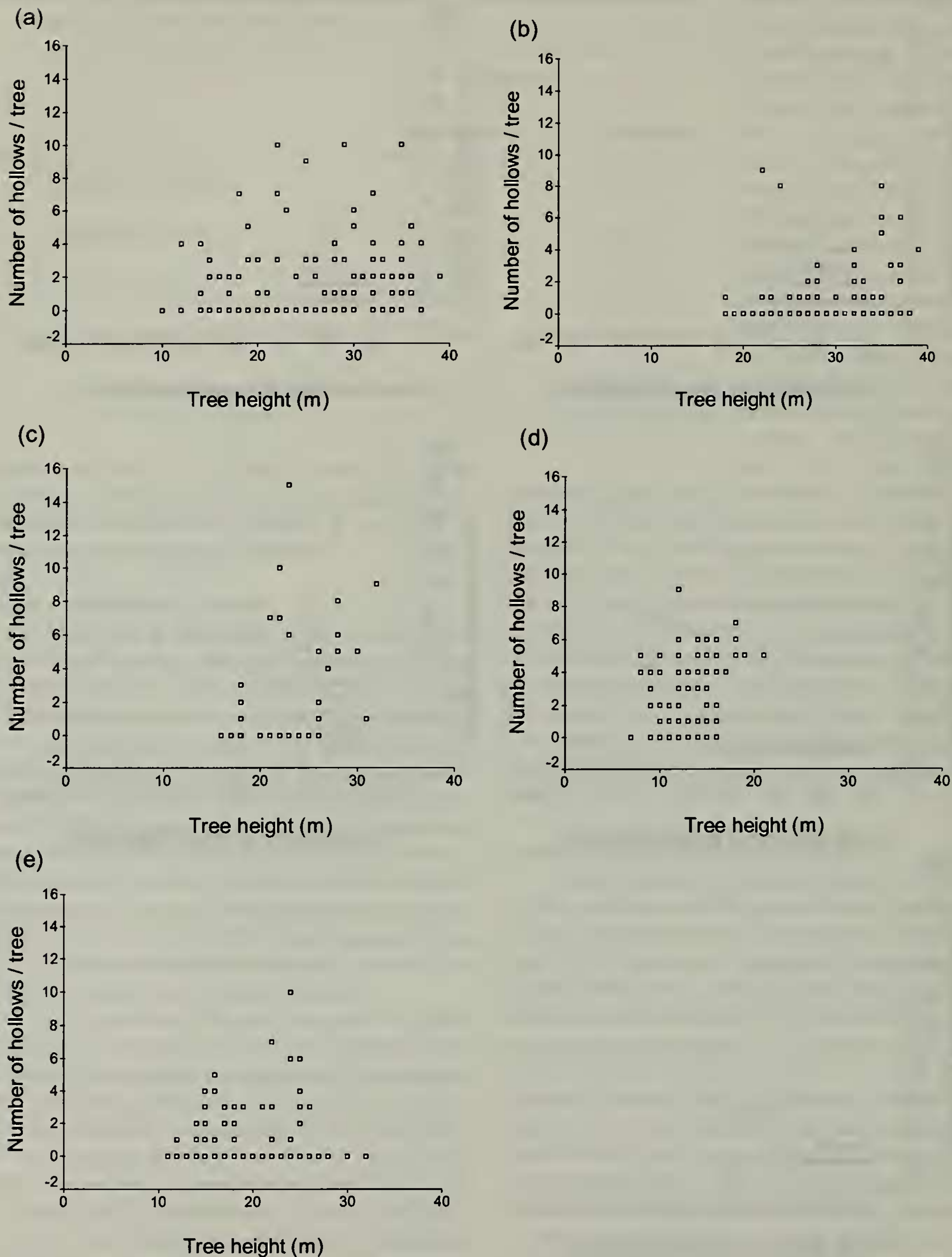

Figure 3. Scatterplots of number of hollows per tree against tree height for (a) *Angophora costata*; (b) *Eucalyptus punctata*; (c) *Eucalyptus pilularis*; (d) *Eucalyptus haemastoma*; and (e) *Corymbia gummifera*.

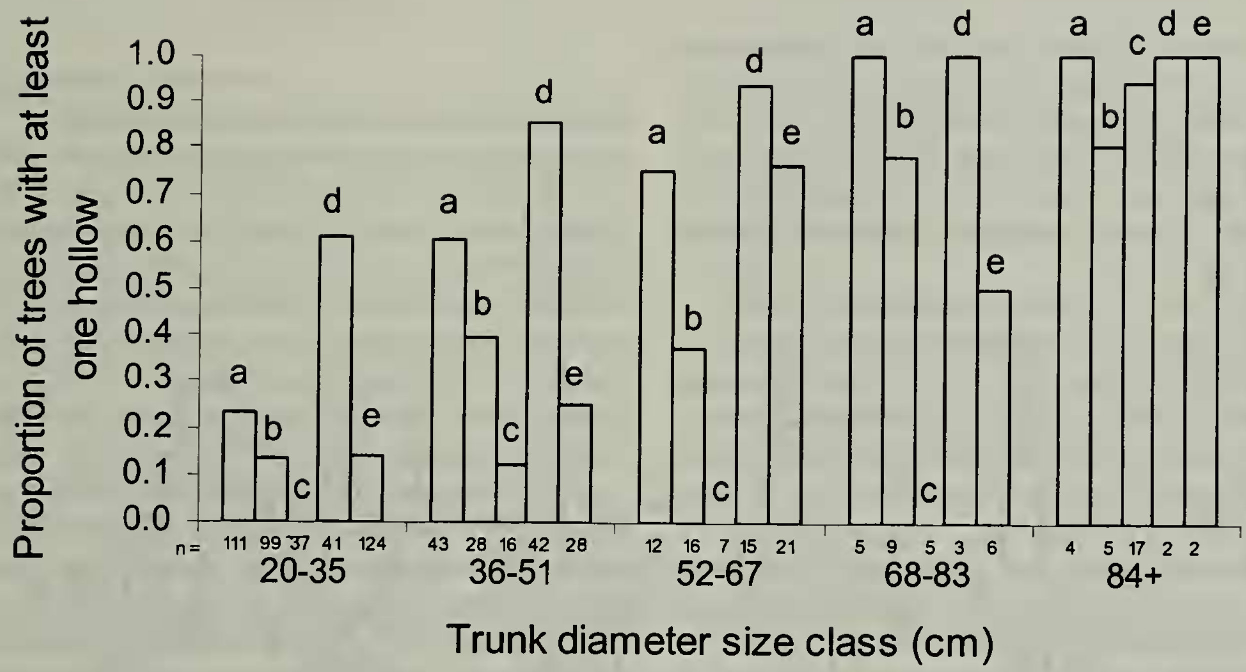

Figure 4. Proportion of hollow-bearing trees in each diameter size class for the five species examined on the Central Coast of NSW (n = number of trees sampled). a = *Angophora costata*; b = *Eucalyptus punctata*; c = *Eucalyptus pilularis*; d = *Eucalyptus haemastoma*; e = *Corymbia gummifera*.

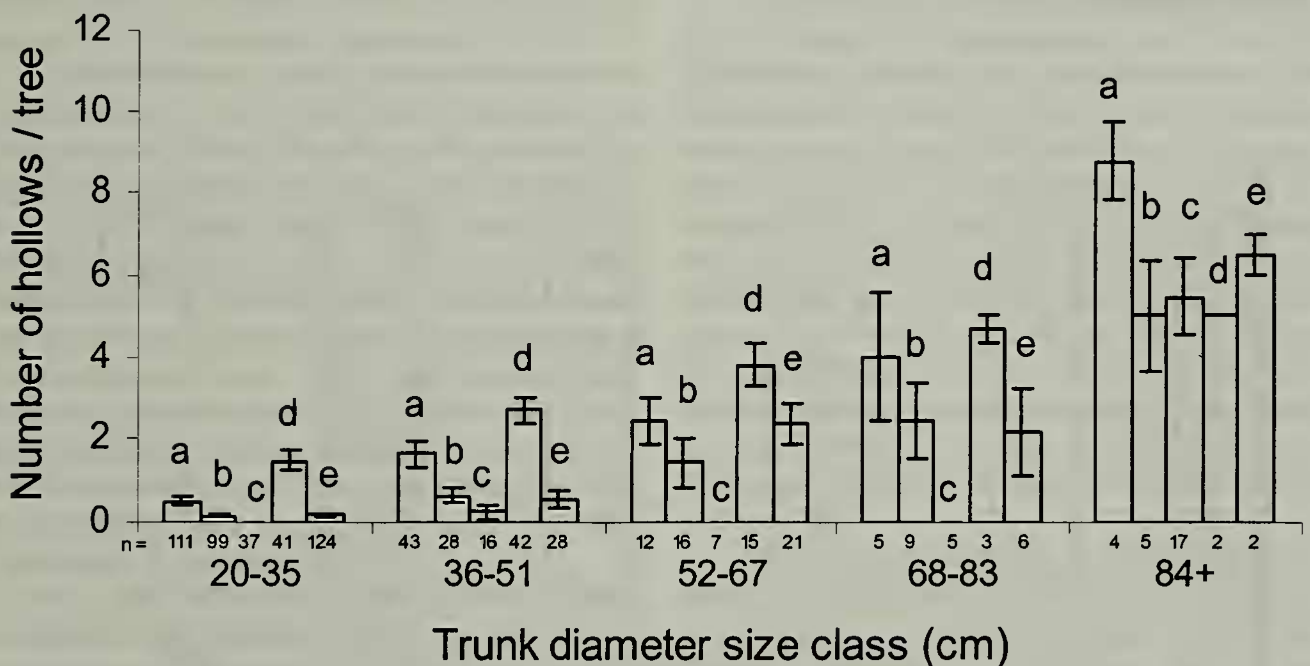

Figure 5. Mean number of hollows per tree in each diameter size class for the five species examined on the Central Coast of NSW (n = number of trees sampled). Vertical bars represent ± one standard error. a = *Angophora costata*; b = *Eucalyptus punctata*; c = *Eucalyptus pilularis*; d = *Eucalyptus haemastoma*; e = *Corymbia gummifera*.

E. pilularis (9 %). The distribution of hollow entrance diameter sizes between branches and main stems was similar. Of the hollows occurring in branches, 26% had a large (> 10 cm) diameter entrance, 27% had a medium (6-10 cm) diameter entrance and 47% had a small (2-5 cm) diameter entrance; of those occurring in the main stem, 24% had large, 21% had medium and 55% had small entrances.

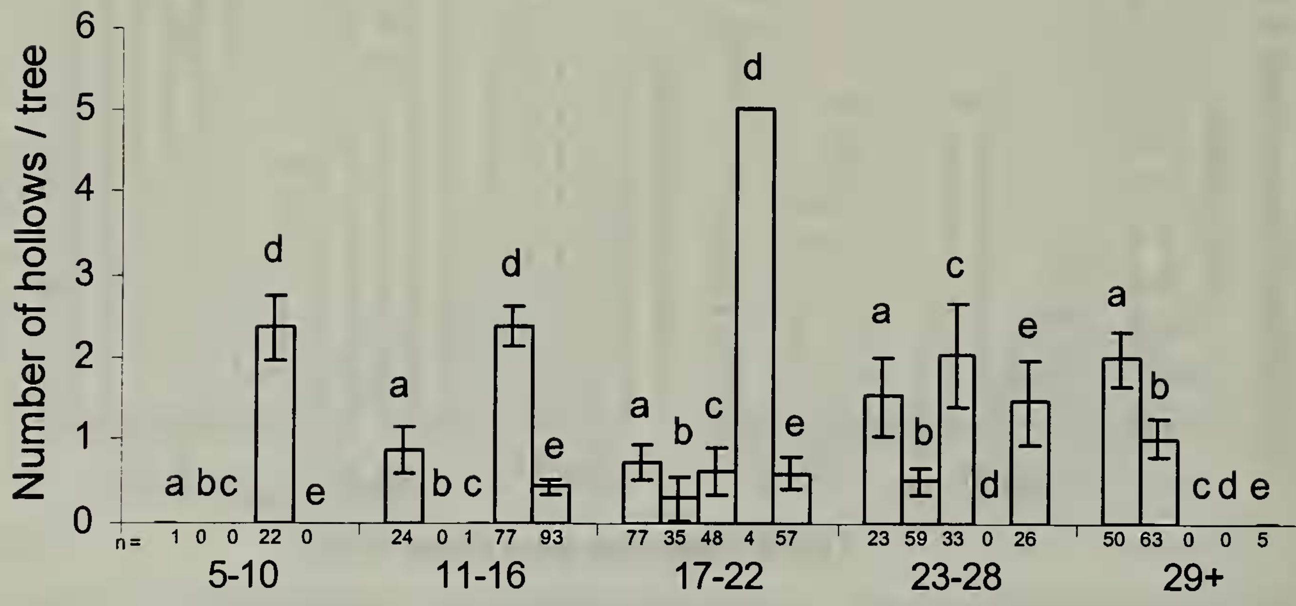

Figure 6. Mean number of hollows per tree in each height size class for the five species examined on the Central Coast of NSW (n = number of trees sampled). Vertical bars represent ± one standard error. a = *Angophora costata*; b = *Eucalyptus punctata*; c = *Eucalyptus pilularis*; d = *Eucalyptus haemastoma*; e = *Corymbia gummifera*.

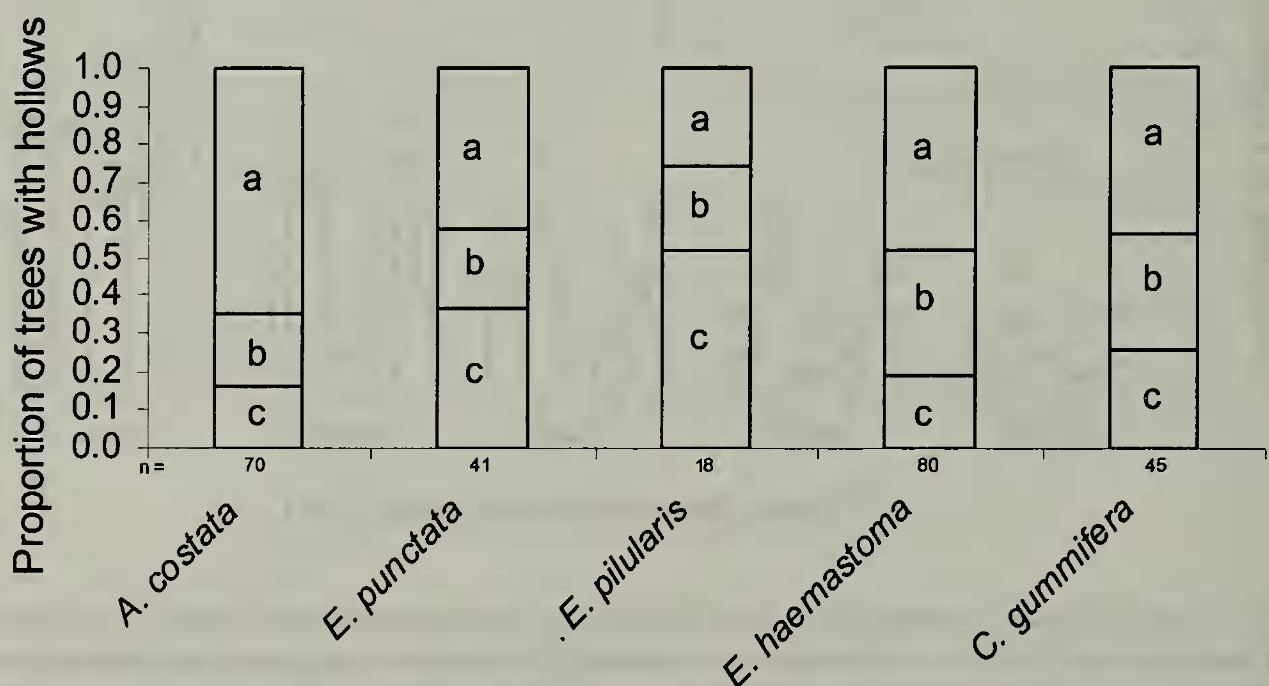

Figure 7. The proportion of hollow-bearing trees with hollows in each entrance size class for the five species examined on the Central Coast of NSW (n = number of trees sampled). a = small (2-5 cm); b = medium (6-10 cm); c = large (>10 cm). See text for full specific names.

DISCUSSION

Abundance of hollows

Most studies of tree hollows use ground-based surveys because climbing trees to measure and record hollow dimensions is impractical (Lindenmayer et al. 1990b; Gibbons et al. 2002) unless a double sampling method is employed (see Harper et al. 2004). Many entrances in trees observed from the ground are blind (i.e. not leading to a cavity suitable for occupation) and thus it is likely that the number of hollows, especially small hollows, is often overestimated (Lindenmayer et al. 1990b). On the other hand, Harper et al. (2004) demonstrated that, on average, ground-based observers correctly identify hollow-bearing trees (where hollows are at least 5 cm deep and have an entrance diameter > 1 cm) 82 % of the time and that hollow frequency is likely to be systematically underestimated. In the current study, it is likely that the number of hollows suitable for fauna have been overestimated because of the large proportion of small hollows encountered and the greater likelihood that small hollows are blind. Therefore, counts of hollows should only be regarded as an "index of hollow availability" (Gibbons and Lindenmayer 2002).

Consistent with previous studies on eucalypts (Lindenmayer et al. 1993a, 2000; Bennett et al. 1994; Gibbons 1994; Gibbons and Lindenmayer 1996, 2002; Williams and Faunt 1997; Gibbons et al. 2000; Wormington et al. 2003), hollow number per tree increased with increasing tree diameter. Older, larger trees are more likely to contain hollows because they are more likely to be repeatedly exposed to events that encourage hollow development, while the decline in growth rate with age is associated with branch shedding, a reduced ability to occlude wounds and an increased chance of heartwood being exposed as sapwood thickness decreases (Gibbons et al. 2000; Gibbons and Lindenmayer 2002).

All of the five species in the current study, with the exception of *Eucalyptus pilularis*, had hollow-bearing trees in the smallest (20-35 cm) diameter size class. However, this does not mean that these hollows are suitable for occupation by fauna. For example, hollow-bearing trees with many hollows are more likely to be occupied by fauna (Gibbons et al. 2002). Thus, smaller diameter trees may be less likely to be occupied because they are more likely to have a lower mean number of hollows per tree (less than two in this study) compared to that of the larger diameter trees (five or more hollows per tree, when dbh ≥ 84 cm). Small diameter trees may also have a smaller number of hollows with large entrances (Wormington et al. 2003) and therefore will suit a narrower range of fauna. The relatively small eucalypt species, *E. haemastoma*, had as many as 60% of trees being hollow-bearing in the 20-35 cm diameter class. This result for *E. haemastoma* supports Gibbons and Lindenmayer (2002) who stated that in regard to hollow formation it is the relative diameter of trees within a species that is important rather than absolute diameter.

The current study found a weak positive association between number of hollows per tree and tree height in four of the five species examined. In contrast, Lindenmayer et al. (2000) found that hollow number decreased with increasing tree height. Their findings may be due to trees in the later stages of senescence having a large number of hollows but were shorter because the tops of their main stem had broken off (Lindenmayer et al. 2000). In our study, only live trees were sampled and the shorter trees belonged to species typically found in nutrient-poor habitats.

Differences in the propensity of species to form hollows

Similar to previous studies (Bennett et al. 1994; Gibbons 1994; Lindenmayer et al. 1993a, 2000; Gibbons and Lindenmayer 1996; Gibbons et al. 2000; Wormington et al. 2003), our study found differences between tree species in abundance of hollows. Species differed in the proportion of trees that were hollow-bearing, the density of hollow-bearing trees at the stand level and in the mean number of hollows per hollow-bearing tree. The proportion of trees (stems > 68 cm) that were hollow-bearing ranged from 63 % for *C. gummifera* to 100 % for *E. haemastoma* and *A. costata*. Similarly, Bennett et al. (1994) found that the proportion of hollow-bearing trees (stems > 70 cm) in the six eucalypts they examined on the northern plains of Victoria ranged from 55 % to 100 %.

Gibbons and Lindenmayer (2002) suggest that trees that "do not reach large diameters, regardless of longevity, are only infrequently observed to contain hollows" and trees < 30 cm dbh rarely contain hollows. This was not the case for *E. haemastoma* in the current study. *Eucalyptus haemastoma* was the shortest of the five species examined, and its diameter did not exceed 85 cm. Being a smaller species, the diameter of a mature *E. haemastoma* tree would be less than that of the other species surveyed. Therefore, smaller diameter *E. haemastoma* trees are likely to have greater susceptibility to fungal decay.

The proportion of *A. costata* trees that were hollow-bearing was relatively high. The heartwood of *A. costata* is "not durable" (Boland et al. 1984), which is consistent with the high number of hollow-bearing trees observed in this species. Gibbons and Lindenmayer (2002) argue that trees with a poor resistance to decay may not be good hollow producers, largely because "a rapid progression of decay may reduce the length of time that hollows persist before the supporting branches fail". Low resistance to decay in *A. costata* and *E. haemastoma* may explain the low proportion of large hollows in these two species, as branches may fail before the small hollows have time to enlarge.

Eucalyptus pilularis was the largest species in this study, but it was also the most variable in size due to few individuals being sampled in the 52-67 cm and 68-83 cm diameter classes. *Eucalyptus pilularis* had a relatively low density of hollow-bearing trees, a low proportion of hollow-bearing trees and a moderate number of hollows per tree. None of the sampled *E. pilularis* trees that were < 36 cm dbh were hollow-bearing, while most trees ≥ 84 cm dbh were hollow-bearing and often contained many hollows. Similarly, Mackowski (1984) found that *E. pilularis* individuals with a diameter less that 100 cm have very few holes, while the number of hollows per tree increases above this size. Heartwood decay is one of the essential precursors for hollow formation (Gibbons and Lindenmayer 2002) and the durability of the heartwood of *E. pilularis* is reported to be "moderate to good" (Boland et al. 1984).

Similar to *E. pilularis, E. punctata* had a relatively low proportion of hollow-bearing trees and a relatively high proportion of hollows with large entrances. Boland et al. (1984) report that the heartwood of *E. punctata* is "extremely durable", which may explain its low proportion of hollow-bearing trees and paucity of trees with multiple hollows. High resistance to decay may also explain the higher proportion of hollows with large entrances, as branches may be less likely to fail before the hollows have time to enlarge.

Corymbia gummifera is a medium-sized tree (11-22 m), which was similar to *E. haemastoma* in that its diameter did not exceed 86 cm. *Corymbia gummifera* had a relatively low proportion of hollow-bearing trees and a low number of hollows per tree. The heartwood of *C. gummifera* is "extremely durable" and the species also has flaky tessellated bark (Boland et al. 1984). These characteristics may protect *C. gummifera* from damage by fire and decay processes that lead to hollow formation and at least partially explain its lower propensity to form hollows. In a study in south-eastern Queensland, Wormington et al. (2003) suggested that the good occlusion ability of *Corymbia citriodora* may explain the low number of hollows observed in trees < 90 cm dbh. The occlusion ability of the species in our study is not known.

Differences between species in the location and entrance size of hollows

Consistent with Gibbons and Lindenmayer (2002), most hollows in this study occurred in branches rather than in main stems. Gibbons and Lindenmayer (2002) reported that main stem hollows accounted for 21-47% of hollows in open forest, 32% of hollows in tall, open forest and rarely occurred in woodlands. Hollows in branches accounted for 49-69% of hollows in open forest, 65% of hollows in tall, open forest and 91% of hollows in woodlands (Gibbons and Lindenmayer 2002). The distribution of hollow locations observed in this study (i.e. 16% of hollows in main stems and 84% in branches) is consistent with the mix of woodland and open forest habitats that were sampled. In agreement with Lindenmayer et al. (2000), branches and main stems in this study supported a fairly even distribution of hollows with small (2-5 cm), medium (6-10 cm) and large (> 10 cm) entrances.

While both *E. pilularis* and *E. punctata* had a relatively low proportion of hollow-bearing trees they had a relatively high proportion of hollows with large entrances suitable for large owls, cockatoos and both large and small marsupials. Further, for *E. pilularis* those trees that were hollow-bearing tended to be of large diameter and have multiple hollows. Thus not choosing a species for retention or planting because of its lower propensity to form hollows may bias against certain groups of fauna; in this case the larger fauna species. *Angophora costata* had a relatively high proportion of hollows with small entrances that would suit smaller marsupials such as squirrel gliders, feathertail gliders and sugar gliders. Although the number of species that can use hollows with small entrance widths (2-5 cm) is limited, a study by Gibbons et al. (2002) in East Gippsland Victoria showed that they were an important hollow resource as they represented 25 % of all occupied hollows. *Corymbia gummifera* had a relatively even distribution of hollows with small, medium or large entrances and therefore had hollows with entrances suited to a wide range of fauna species.

Hollow characteristics (i.e. number, density, size, spacing, location) are not the only factor to consider when choosing habitat trees for retention or planting. Although *E. punctata* was one of the species with a lower propensity to form hollows, it did contain hollows and is an important sap tree for the yellow-bellied glider (Goldingay 2000). Similarly, *E. pilularis* provides winter nectar and *C. gummifera* provides sap and summer nectar for squirrel gliders (Smith and Murray 2003).

In conclusion, the number of hollows per tree was positively related to tree size and clearly hollow abundance will be low where few large trees are found. Timber removal prior to 1967 in Bouddi National Park and prior to 1999 in Ourimbah State Forest may have affected the *E. pilularis* population sampled in this study. Thus the data shown here for *E. pilularis* is not representative of hollow availability in 'undisturbed' vegetation, particularly as this species is likely to have been preferentially removed. The five tree species examined did differ in their propensity to form hollows. The relative diameter at which hollows form was shown to be important, with the smallest eucalypt species (*E. haemastoma*) observed to have a substantial number of hollows at tree diameters less than those often considered in hollow resource assessments. Given the diversity of hollows required by hollow-dependent fauna, and the many variables affecting the development of hollows, the retention of a mix of tree species should be favoured to supply this critical resource.

ACKNOWLEDGMENTS

We would like to thank the NSW National Parks and Wildlife Service and Forests NSW for permission to sample within their areas of jurisdiction. Particular thanks go to Adam Fawcett of Forests NSW. The manuscript benefited from the comments of two anonymous reviewers.

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